THE WILSON BULLETIN
A QUARTERLY JOURNAL OF ORNITHOLOGY
Published by the Wilson Ornithological Society

VOL. 115, NO. 3 September 2003 PAGES 225–356

Wilson Bull., 115(3), 2003, pp. 225–230

COMPARATIVE RELATIONSHIPS AMONG EYE COLOR, AGE, AND SEX IN THREE NORTH AMERICAN POPULATIONS OF COOPER'S HAWKS

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ABSTRACT.—Although adult plumage in Cooper's Hawks (*Accipiter cooperii*) exhibits little or no sexual dichromatism, iris color reportedly changes from yellow or light orange in younger birds to shades of orange or red in older birds, especially in males. However, there is little quantitative data on this phenomenon. It has been suggested that male eye color may serve as a signal of age and hence reproductive fitness and thus offer a basis for nonrandom mating in Cooper's Hawks. In this study we examine the relationships between eye color and age, sex, and reproductive output for Cooper's Hawks in two breeding populations in British Columbia and North Dakota, 1999–2002, and compare these results to those previously published for a breeding population in Wisconsin, 1980–1995. Cooper's Hawks in British Columbia and North Dakota appear to acquire darker orange or red irides more frequently and more quickly than their counterparts at known and relative ages in Wisconsin. Females in all study sites are slower and less likely than males to acquire the darkest eye colors. Eye color is not a reliable predictor of age in individual male and female Cooper's Hawks, for researchers and perhaps for the birds themselves, because individual hawks of a given eye color displayed variation in known and relative ages in British Columbia and Wisconsin. There was no significant relationship between the eye color of males and their brood sizes in any of these three populations, and therefore no discernable support for the premise that male eye color *per se* signals male fitness, or functions as a sexual trait for assortative mating in this species. *Received 20 January 2003, accepted 3 June 2003.*

In the Cooper's Hawk (*Accipiter cooperii*), a species with little or no sexual dichromatism in adult plumage (Rosenfield and Bielefeldt 1993), iris color shows an age dependent relationship, especially in males, with irides typically changing from yellow or light orange in younger birds to shades of orange or red in older birds (Rosenfield et al. 1992, Rosenfield and Bielefeldt 1997). Other researchers, although lacking multiyear data on eye color of individually marked birds of known age, have postulated that eye color may be a characteristic (Snyder and Snyder 1974) or one of a suite of characteristics (Boal 2001) that might signal reproductive fitness and offer the opportunity for assortative mating, but we found no correlation between male eye color and clutch or brood sizes as indices of fitness in a population in Wisconsin (Rosenfield et al. 1992, Rosenfield and Bielefeldt 1997). However, the relationships between eye color and

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TABLE 1. Iris color of relative-age[a] Cooper's Hawks breeding in British Columbia during 1999–2002, and mean eye color scores (in parentheses) for corresponding relative-age birds in Wisconsin, 1980–95.[b]

	Eye color categories						
	1 Yellow	2 Light orange	3 Orange	4 Dark orange	5 Red	*n*	Mean eye color score
Males							
ASY	0	0	7	7	11	25	4.2 (3.6)
A3Y	0	0	0	3	4	7	4.6 (3.7)
A4Y	0	0	0	1	3	4	4.8 (4.2)
A5Y	0	0	0	0	1	1	5.0 (4.7)
A6Y	0	0	0	0	1	1	5.0 (4.8)
A9Y	0	0	0	0	1	1	5.0 (5.0)
Females							
ASY	0	1	8	12	2	23	3.6 (2.8)
A3Y	0	0	1	6	1	8	4.0 (2.9)
A4Y	0	0	2	2	0	4	3.5 (3.1)
A5Y	0	0	1	1	0	2	3.5 (3.3)

[a] Relative-age birds are ASY (after-second-year) birds two or more years of age, and recaptures of these individuals (A3Y, A4Y, etc.) in subsequent years.

[b] Mean eye color scores for Wisconsin birds previously reported by Rosenfield and Bielefeldt (1997).

age, sex, and reproductive output are unreported for Cooper's Hawks elsewhere in eastern North America, or in western populations that are morphometrically separable from Wisconsin birds (JB, MAB, RKM, LJR, RNR, and ACS unpubl. data). Here we show that patterns of change in eye color with age and sex differ between Wisconsin birds and breeding birds in two western populations in British Columbia and North Dakota.

STUDY AREA AND METHODS

Previous results and methods in Wisconsin (44° 25′ N, 89° 30′ W), 1980–1995, are described in Rosenfield and Bielefeldt (1997). During 1999–2002 we applied the same methods at 45 nests in western North Dakota (48° 37′ N, 102° 27′ W), and at 85 nests on Vancouver Island, British Columbia (48° 27′ N, 123° 21′ W). For descriptions of western study areas see Murphy (1993) and Stewart et al. (1996). In North Dakota we trapped breeding Cooper's Hawks at nests, including 38 males and 31 females captured only once. In British Columbia we caught 47 individual males and 42 individual females and retrapped some of the same birds a total of 38 times in subsequent years; 51 captures and recaptures in British Columbia involved 43 individual breeding birds of known age originally captured as SY (second year) birds or marked as nestlings during 1995–2001. Relative-age birds of unknown age are classified as ASY (after second year) birds that are two or more years of age upon initial capture; recaptures of these individuals are designated A3Y, A4Y, etc., in subsequent years.

We designated eye color of captured hawks as yellow, light orange, orange, dark orange, or red following Rosenfield et al. (1992). We determined mean eye color scores for hawks in a relative age category through assignment of corresponding numerical scores of 1–5 for yellow through red eyes, respectively (Rosenfield et al. 1992). As in Wisconsin (Rosenfield and Bielefeldt 1997), we determined brood sizes in British Columbia and North Dakota by climbing to nests at the mid-nestling stage (about 16 days of age). We calculated probability values using SYSTAT (Wilkinson 1992) and StatXact-Turbo (Mehta and Patel 1992). Significance was accepted at $P < 0.05$.

RESULTS

On the British Columbia study area, in both sexes, iris color changed from lighter shades of yellow or orange in younger birds to darker shades of orange or red in older birds. This result held true for both relative-age and known-age birds (Tables 1, 2). Males exhibited a greater mean eye color score (i.e., darker eyes) than females of the same relative age in both British Columbia and North Dakota (Tables 1, 3). These results concur with pre-

TABLE 2. Iris color of known-age Cooper's Hawks breeding in British Columbia during 1999–2002 and in Wisconsin (in parentheses), 1980–2002.[a]

Age in years	Eye color categories				
	1 Yellow	2 Light orange	3 Orange	4 Dark orange	5 Red
Males					
1	0 (2)	0 (8)	0 (1)	0 (0)	0 (0)
2	0 (0)	0 (3)	1 (12)	5 (2)	0 (0)
3	0 (0)	0 (2)	1 (5)	3 (3)	6 (1)
4	0 (0)	0 (0)	0 (3)	1 (3)	7 (2)
5	0 (0)	0 (0)	0 (0)	0 (2)	4 (1)
6	0 (0)	0 (0)	0 (0)	0 (1)	2 (0)
Females					
1	6 (12)	2 (2)	3 (0)	0 (0)	0 (0)
2	0 (0)	0 (2)	2 (0)	1 (0)	0 (0)
3	0 (0)	0 (1)	1 (2)	1 (0)	0 (0)
4	0 (1)	0 (0)	1 (1)	2 (0)	0 (0)
5	0 (0)	0 (1)	0 (1)	1 (0)	0 (0)
6	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
7	0 (0)	0 (0)	0 (0)	1 (0)	0 (0)

[a] Includes seven Wisconsin birds (1996–2002) that were not reported in Rosenfield and Bielefeldt (1997).

viously reported data for Cooper's Hawks in Wisconsin (Rosenfield and Bielefeldt 1997).

We assume that our samples of relative-age birds recaptured in subsequent years (Table 1) and individual ASY birds (Table 3) exhibit similar age distributions among breeding adults in mark-recapture studies in Wisconsin (Rosenfield and Bielefeldt 1997; JB, LJR, and RNR unpubl. data), in British Columbia (ACS unpubl. data), and in North Dakota (RKM unpubl. data). If so, adults of both sexes have significantly more ASY birds in darker eye color categories (dark orange and especially red) in British Columbia and North Dakota than in Wisconsin (Table 3). Proportions of dark orange and red eyes in both ASY males (83%) and ASY females (63%) were much greater in British Columbia and North Dakota than in Wisconsin (49% males, 19% females). In contrast to Wisconsin, where 24% of breeding ASY adults in combined sexes had yellow or light orange eyes, less than 2% (two individuals) had these lighter shades in British Columbia and North Dakota (Table 3).

In British Columbia, relative-age birds recaptured one or more times after initial capture (Table 1) also had predominately dark orange or red eyes in males (100%, $n = 14$ recaptures) and females (71%, $n = 14$ recaptures). Mean eye color score in both sexes increased with relative age in British Columbia and exceeded the mean score at the same relative age in Wisconsin in all but one case (an A9Y male) for both sexes (Table 1). Lack of independence among recaptures of relative-age birds prohibited inferential analysis of mean scores.

Breeding birds of known age in British Columbia appear to attain dark orange or red eyes more frequently and more rapidly than

TABLE 3. Iris color of ASY[a] Cooper's Hawks breeding in British Columbia (BC) and North Dakota (ND), 1999–2002, and Wisconsin (WI), 1980–95.[b] Percentages are in parentheses. Significant differences were found among eye color categories in ASY birds among all three study areas in males (Fisher's exact test, $P = 0.0005$) and females (Fisher's exact test, $P = 0.0005$), and between BC males and females ($P = 0.04$) and ND males and females ($P = 0.008$). No significant differences were found between eye color categories of BC and ND ASY males ($P = 0.19$) or females ($P = 0.89$).

	Eye color categories						
	1 Yellow	2 Light orange	3 Orange	4 Dark orange	5 Red	*n*	Mean eye color score
Males							
BC	0	0	7 (28)	7 (28)	11 (44)	25	4.2
ND	0	0	4 (11)	16 (42)	18 (47)	38	4.4
WI	0	15 (11)	57 (40)	46 (32)	24 (17)	142	3.6
Females							
BC	0	1 (4)	8 (35)	12 (52)	2 (9)	23	3.6
ND	0	1 (3)	10 (32)	16 (52)	4 (13)	31	3.7
WI	9 (5)	53 (29)	87 (47)	33 (18)	2 (1)	184	2.8

[a] ASY (after-second-year) birds are two or more years of age at initial capture.
[b] Samples from Wisconsin previously reported by Rosenfield and Bielefeldt (1997).

TABLE 4. Mean brood size by eye color category for breeding male Cooper's Hawks and by age structure of mated pairs in North Dakota and British Columbia, 1999–2002. Sample sizes are in parentheses.

Mated pair age[a]	Eye color categories 3 Orange	4 Dark orange	5 Red	*U*	*P*
British Columbia					
Gray males mated to gray females	4.0 (6)	3.89 (9)	3.85 (20)	0.014	0.99
Gray males mated to gray or brown females	4.0 (6)	3.73 (15)	3.83 (24)	0.103	0.99
North Dakota					
Gray males mated to gray females	3.75 (4)	2.88 (17)	3.13 (16)	2.997	0.22

[a] Gray and brown birds are those individuals ≥2 years of age and one year old, respectively.

their counterparts in Wisconsin (Table 2). For example, no known-age males in British Columbia had light orange eyes at >2 years of age, but 5 (18%) of 28 males captured and recaptured in Wisconsin had light orange eyes at 2–3 years of age. In British Columbia, 79% of males captured and recaptured at age 3–6 years (n = 24) had red eyes, but only 17% of those in Wisconsin (n = 23) had red eyes. Forty-three percent of known-age males captured and recaptured in British Columbia (n = 30) acquired red eyes by ages 3–4, but only three males (6%) had red irides by these ages in Wisconsin.

In comparison to Wisconsin birds, known-age female hawks in British Columbia also appear to show quicker and more frequent changes toward darker irides (Table 2). Six (29%) of 21 females captured or recaptured in British Columbia had dark orange eyes at ages 2–7, while all of 9 females of the same age captured and recaptured in Wisconsin had eyes that were orange or lighter (Table 2).

We found no significant differences in brood sizes among male eye color categories in North Dakota in a sample composed exclusively of ASY, gray-plumaged adults (Table 4). Mean brood size did not vary by more than 0.87 nestlings among male eye color categories despite brood sizes that ranged from 1–4 young in North Dakota. There also were no significant differences in brood sizes among male eye color categories in British Columbia in gray-plumaged ASY pairs or in ASY males paired with brown-plumaged, second-year (SY) females (Table 4). Brood size in British Columbia varied from 1–5 young, but mean brood size among male eye color categories differed by only 0.15 and 0.27 nestlings in ASY-ASY and ASY-SY pairs, respectively. Because of small brood size samples in the orange eye color category in British Columbia and North Dakota, we also tested for differences in mean brood size between the dark orange and red eye color categories; we did not detect significant differences in either study area (all $P > 0.50$). As previously reported (Rosenfield and Bielefeldt 1997), mean brood (as well as clutch) sizes also failed to show significant differences among male eye color categories in Wisconsin.

DISCUSSION

We have shown that breeding Cooper's Hawks in British Columbia and North Dakota appear to acquire darker orange and red irides more frequently and more quickly than their counterparts of known and relative ages in Wisconsin. Despite these differences among three morphometrically separable populations of the species, with both British Columbia and North Dakota birds smaller than Wisconsin birds but comparable to each other in size (LJR et al. unpubl. data), similar sexual disparities in eye color persist among British Columbia, North Dakota, and Wisconsin populations. In general, females are slower and less likely than males to acquire the darkest iris colors, and some of the oldest females had not yet acquired red eyes at ages of up to A9Y (Tables 1–3; Rosenfield and Bielefeldt 1997).

It is conceivable that populations in British Columbia and North Dakota might show delayed breeding in comparison to Wisconsin birds, so that our samples of relative-age (Table 1) and ASY (Table 3) hawks in British Columbia and North Dakota might be construed to show that younger males as known-

age breeders were more numerous in Wisconsin than in British Columbia. However, even if delayed breeding were to occur in British Columbia, known-age males there acquired darker eyes more frequently and more rapidly than males of the same age in Wisconsin (Table 2). Therefore, the possibility of delayed breeding in British Columbia does not compromise our conclusion about eye color in known-age birds. We thus assume that any possible effects of delayed breeding also would have minimal effects on our conclusions regarding ASY birds in the three study populations. As in Wisconsin (Rosenfield and Bielefeldt 1997), eye color in British Columbia is not a reliable predictor of age in individual male and female hawks, for researchers and perhaps for the birds themselves, because individuals in the same eye color category displayed variation in known or relative ages (Tables 1, 2).

Because male Cooper's Hawks are the principal provider of prey to females and young during preincubation, incubation, and nestling stages (Rosenfield and Bielefeldt 1993), we have used clutch and brood sizes as indices of provisioning abilities and hence male fitness (Rosenfield et al. 1992, Rosenfield and Bielefeldt 1997). Noting that male eye color darkens in older birds, Snyder and Snyder (1974: 221) suggested that darker eyes "could be a good indicator" of hunting abilities and male fitness as well as male age. However, using brood sizes as an index, we found no significant relationships between eye color in males and their brood sizes in North Dakota or British Columbia (Table 4) or Wisconsin (Rosenfield and Bielefeldt 1997), and thus no discernable support for the premise that male eye color *per se* signals male fitness.

It is possible that human perception of colors do not correspond to those of birds (Mahler and Kempenaers 2002); some species, including some raptors (Viitala et al. 1995), are sensitive to near-ultraviolet wavelengths. We are unable to dismiss that possibility in this analysis. Even so, using human perception in eye color analyses prompted by prior propositions (Snyder and Snyder 1974, Boal 2001) that assortative mating may occur on the basis of age and eye color in Cooper's Hawks, we were unable to detect any relationship between male eye color and male fitness. We have demonstrated that nonrandom mating in Cooper's Hawks in Wisconsin is related to variations in body mass and wing chord, and that such assortative mating does carry positive fitness consequences, including recruitment, for some pairs (Rosenfield and Bielefeldt 1999). If nonrandom mating on the basis of eye color were to occur in Cooper's Hawks, we could not detect selective benefits in our study of three North American populations, despite the variation in pace of eye color change and the varied proportion of darker irides among these populations. Although some studies have succeeded in discovering patterns of assortative mating using sexual traits in univariate approaches (e.g., Andersson 1982, Smith and Montgomerie 1991, Olsen et al. 1998, Rosenfield and Bielefeldt 1999, Regosin and Pruett-Jones 2001), Badyaev and Qvarnstrom (2002) have cautioned that ecological settings and behaviors in combination with single sexual traits may be involved in mate choice in birds.

ACKNOWLEDGMENTS

We thank T. Booms, J. Clarke, K. Collins, W. Cornatzer, D. Hill, N. Horne, G. Grondahl, B. Mackie, B. and I. Stewart, W. Stout, and D. Svingen for their logistical support and field assistance. An anonymous referee and C. Boal provided useful comments on this paper. Funding was provided by the Biology Dept., the Personnel Development Committee, the Letters and Science Foundation, and the Wisconsin Coop. Fishery Unit at the Univ. of Wisconsin-Stevens Point; the BC Conservation Data Centre; the Municipality of Saanich Parks Dept. (British Columbia), the BC Habitat Conservation Trust Fund; the Nongame Wildlife Program of the North Dakota Game and Fish Dept.; the U.S. Forest Service, the U.S. Fish and Wildlife Service; and the North Dakota, Wisconsin, and Great Lakes Falconers associations.

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